Population Dynamics of the Cotton Rat in Southeastern Virginia

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ABSTRACT

We used monthly live trapping for 2.5 years to evaluate the life-history features of the most common small mammal, *Sigmodon hispidus* (hispid cotton rat), in an old field at its northern limit of distribution on the Atlantic Coast. Peak densities, achieved in late autumn or early winter, were among the highest recorded for the species and were more typical of geographically marginal populations rather than of central ones. Unlike some other marginal populations, hispid cotton rats in southeastern Virginia did not lose significant body mass over the winter (when few juveniles were present) and survival in winter was not significantly different from that of other seasons, perhaps due to the moderating effects on winter temperatures of the nearby Atlantic Ocean and Chesapeake Bay. Our study provides support for the presence of spring and autumn cohorts, with long-lived animals being drawn almost entirely from the latter.

INTRODUCTION

Sigmodon hispidus Say and Ord (hispid cotton rat), a 100-g herbivorous rodent, is the sole member of a tropical genus broadly distributed across the southern US, for which the northward expansion of its distributional range into the central states and along the Atlantic Coast is well known (Cameron and McClure, 1988). Since the first Virginia report (Patton, 1941), it has spread across southern Virginia and into the Piedmont (Pagels and Moncrief, 2015), and likely is spreading northward wherever its movements are not impeded by large rivers or the Chesapeake Bay. Although much studied across its distribution, capture-mark-recapture (CMR) studies that provide the most useful information on demographic features are limited to those in Florida (Layne, 1974; Stafford and Stout, 1983), Texas (Cameron and colleagues), Oklahoma (Goertz, 1964; McMurray et al., 1994; Schetter et al., 1998), eastern Kansas (Slade and colleagues), and western Kansas (Fleharty et al., 1972); this report provides demographic information for a marginal population in coastal Virginia.

Unlike many temperate rodents, the population biology of the hispid cotton rat (hereafter, cotton rat) is highly variable across its distribution, with some populations showing high breeding activity in spring and autumn, and others only in autumn (Cameron and McClure, 1988). Peak densities in late autumn, the usual pattern for north temperate rodents, are reported

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in some populations, but a population in Florida had a peak in August and still others had December or January peaks. Numerous studies report extirpations or near extirpations of local populations in Oklahoma, Kansas, and Tennessee (Dunaway and Kaye, 1961; Goertz, 1964; Sauer, 1985; Langley and Shure, 1988; Clark et al., 2003), an indication of a lack of adaptation to severe cold. Further, cotton rats in these northern regions often lose body mass over the winter (Dunaway and Kaye, 1961,1964; Goertz, 1965; Chipman, 1966; Slade et al., 1984; Schetter et al., 1998) but adults in other populations (e.g., Georgia, Virginia) maintain or gain body mass during winter (Bergstrom and Rose, 2004; Green and Rose, 2009). Sex ratios often deviate from unity, and in unpredictable ways.

The objective of our study was to provide demographic details for a population of cotton rats from southeastern Virginia, based on monthly live trapping across a 2.5-year period that included 3 winters, including patterns of density, sex ratio, body mass, and residency, plus length of reproductive seasons, proportions of transients, and lifespan (longevity).

MATERIALS AND METHODS

Description of field site – Our study site was an old field owned The Nature Conservancy located in southern Chesapeake (37º50'N, 76º20'W), Virginia. When we began the field study in December 2002, the land had been withdrawn from agricultural production for 2 years and was dominated by chest-high little bluestem (*Schizachyrium scoparium*) with other associated grasses, mostly panic grasses (*Panicum* spp.), and with short volunteer trees, mostly loblolly pine (*Pinus taeda*). The 11.5-ha field was bordered on the north and east by mature hardwood forest, on the west by a road and mature pines beyond that, and on the south by a freshwater marsh. The study grid was bisected by a meter-wide and 0.5 m-deep drainage ditch that filled during the winter months, typical of this region of high water table. The site lies about 4 km east of the Great Dismal Swamp National Wildlife Refuge.

Field methods – We trapped for 3 days each month from December 2002 through July 2005, except for June 2003 when extreme predator disturbance required closing the traps. Our study grid was 8 by 8 with 12.5-m intervals, producing a grid with an effective trapping area of 1 ha (Stickel, 1954). At each grid coordinate we placed 2 Fitch live traps (Rose, 1994) baited with a mixture of wild bird seed and sunflower seeds, with fiberfill added in winter for insulation. We set traps in the late afternoon, usually during the new moon phase, and checked them early for the next 3 mornings. From April through October, we locked the traps open in the morning and reset them again just before sundown to prevent heat-related mortality in the traps. Mortality for rodents was nearly zero.

Each small mammal was given a right ear tag with unique number, which, if lost, was replaced with a tag in the left ear, and the animal was synonymized to avoid inflating estimates of density. We recorded information on reproductive condition of males using abdominal testes (not fertile) versus descended testes (fertile). We evaluated 3 reproductive features in females: not perforate or perforate vaginal orifice, small-medium-large nipple size, and closed-slightly open-open pubic symphyses; the latter conditions in each category are associated with reproduction. We used a Pesola™ pencil-scale to determine body weight (g), then released the animal at the coordinate of capture. We collected the same information for recaptured animals,

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although within a month only next coordinate was recorded. Our goal was to mark all animals and follow events of their lives. We defined juveniles as those < 50 g, sub-adults as 51–100 g, and adults as those > 100 g.   We used a 50-g criterion as the upper limit for juveniles because our earlier necropsy studies had revealed fertile males and pregnant females weighing less than 60 g in populations from southeastern Virginia (Rose and Mitchell, 1990; Bergstrom and Rose, 2004). We designated 3 residency classes: transients (seen only in 1 month), visitors (seen in 2 months), and residents ($\geq$ 3 months).

We conducted our study before our university IUCAC required approval for field studies of wild mammals.   Our methods followed the guidelines for the use of mammals in research, as outlined by the American Society of Mammalogists, the latest version of which is Sikes et al. (2016).

Statistical analyses – We used SPSS version 12.0 (2003; SPSS, Inc., Chicago, Illinois) for analysis. Mean masses for both sexes were calculated for month and season. We defined winter as December-February, spring as March-May, summer as June-August, and autumn as September-November.

We used Chi-square tests to determine deviations from unity in sex ratios and to test for differences among the three residency classes. We determined density using the JOLLY (Hines, 1996) software package, which uses the Jolly-Seber model, and also calculated density by hand using minimum number known to be alive (MNA: Krebs, 1966), which is calculated by adding the number of individuals captured during month *t* to those tagged animals but not captured in month *t* but known to have survived to month *t* + 1 or beyond. Importantly, we trapped beyond February 2005 (the end of our period of analysis) because the population estimators require the numbers of animals captured months later to enable accurate calculations.   Thus, we monitored the decline of the population after February 2005 but present only anecdotal or qualitative information from the spring-early summer 2005 period.

We used correlation analysis to examine the concordance of the 2 methods of estimation and also used the density values produced by JOLLY to evaluate a possible correlation between the first and second year of the study. We used Student's *t*-tests to detect sexual dimorphism and two-sample *t*-tests to examine body mass differences between years. We analyzed mean mass using a model-I two-factor analysis of variance (ANOVA) to observe any potential significant differences between sexes and among months. We used REGWF multiple range tests to identify important variables for each ANOVA for which factors were significant (SPSS, 2003).

RESULTS

We tagged 864 different small mammals of 8 species in 9088 trapping nights, of which *Sigmodon hispidus* accounted for 513 (59.4%) individuals. (Table 1 shows the sum of the tagged animals caught each month and the number in parenthesis includes recaptures within a month.) Meadow voles (*Microtus pennsylvanicus*) and eastern harvest mice (*Reithrodontomys humulis*) were sub-dominant members of the community. The other mammals were much less common and sometimes their presence was brief (e.g., no house mice, *Mus musculus*, after May 2003) or

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intermittent (marsh rice rats, *Oryzomys palustris*, were present mostly in the cool months, often also the wettest ones).

Population density – Using the best-fit model (Jolly-B: $X^2 = 46.29$, $df = 33$, $P = 0.062$) for this population, density in late winter 2003 was estimated to be about 60 cotton rats/ha, but numbers dropped by half that spring before recovering to comparable density in late summer (Fig. 1). By the end of the autumnal breeding season, population density had exceeded 100/ha at the start of the second winter. The highest densities (124/ha) were achieved in January 2005, in part due to the breeding season extending into November in 2004. The decline in February 2005 continued into spring and summer and when we ended monthly trapping in July 2005, only a few cotton rats remained (we caught three in July). The Pearson's correlation between JOLLY and MNA values was highly significant ($r = 0.963$, $n = 25$, $P < 0.001$), validating the density estimate of either method.

Sex ratios – The sex ratio (248 males: 265 females) of all tagged cotton rats was not different from unity ($X^2 = 0.56$, $P > 0.50$). However, tagged females were trapped in more successive months than males, so when all tagged cotton rats caught at least once per month are considered, we captured significantly more females than males (652:538; $X^2 = 10.92$, $P < 0.001$).   This ratio is unusual because in most small mammal studies, captures of males outnumber those of females by approximately 3:2.

Age distributions – Across the study, juveniles comprised 13 % of each sex. Thus, the population was dominated by sub-adult and adult cotton rats. During the first 2 winters, less than 5 % of cotton rats were juveniles and in the third winter no juvenile was present.

Patterns of residency – Our population showed a high proportion of residents: 72 percent (Table 2), and thus relatively low proportions of transients and visitors. For visitor and resident classes, some tagged animals were absent or not captured for 2 or 3 months and then returned to the trappable population (7% of males, $n = 17$, and 6% of females, $n = 15$). Female residents were significantly more numerous than male residents (543 versus 428: $X^2 = 13.62$, $P < 0.001$) but more male than female transients were recorded ($X^2 = 6.95$, $P < 0.05$).

Patterns of reproduction – Distinctive breeding and non-breeding seasons were evident based on external features of both sexes. In all 3 winters, neither males nor females showed signs of breeding, but by March males had descended testes and by April about two-thirds of females had perforate vaginae and enlarging nipples. Females gradually increased their level of reproduction from August through the end of the year. Testicular regression, begun in October, was completed by December. This population was characterized by few young being raised in spring or early summer but greatest recruitment occurring in autumn, and extending into January in the last year.

Patterns of body mass – For an assessment of body mass, we considered only those cotton rats $\geq$ 50 g in the analysis and also excluded obviously pregnant females. Because each tagged sub-adult and adult cotton rat likely has a different body mass each month, we included each weight at first capture of a month in calculations of body mass. The mean body mass for males was 99.51 ± SE 1.327 g ($n = 466$) and 92.23 ± SE 1.132 g ($n = 522$) for females. These means were significantly different ($t = 4.007$, $P = 0.001$). Further, males were significantly heavier in 2003

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(104.71 ± SE 2.002 g) than in 2004 (97.92 ± SE 2.218 g; $t = 1.931$, $P = 0.054$), but females had nearly identical mean masses in both years. Male residents were significantly heavier that male transients ($t = -2.655$, $P = 0.01$) but female residents and transients were of similar size.

A model-I two-factor ANOVA using sex and months as factors on log-transformed data confirmed the significant mass differences between the sexes ($F = 7.451$, $df = 1959$, $P = 0.006$) and also significant differences among months ($F = 4.97$, $df = 25,958$, $P = 0.001$). The sex-month interaction term was also significant ($F = 2.046$, $df = 22,958$, $P = 0.03$).

Despite no significant differences in mean mass for winter months, as demonstrated by the REGWF tests from the model-I two-factor ANOVA on monthly values, we observed slight, irregular variations in mean mass in all 3 winters (Fig. 2). The mean mass of females was stable in 2 winters but decreased slightly in the second winter. Males were more erratic, gaining body mass the first winter, losing some the second winter, and holding constant mass the third winter. Overall, masses of both males and females were nearly constant over the winter months.

Longevity – We examined the lifespans of the 12 males and 21 females recorded on the grid for 6 or more months; their mean longevity was similar, 7.2 and 7.5 months, respectively. Except for those tagged in December at the start of the study, most long-lived cotton rats were tagged at juvenile body masses, usually 20–40 g. One adult female, first caught in October 2003, was captured multiple times, had litters in May and October 2004, and likely was born in April or May 2003, making it about 20 months old when last caught in January 2005.

DISCUSSION

We observed peak densities in late autumn or early winter, with ~60/ha, 100/ha and 124/ha in the 3 years, with declining densities through winter but with lows not dipping below about 30/ha during the first 2 springs. However, at the end of the study, the pines had shaded out the grasses, greatly diminishing the monocot-rich diet of cotton rats (Walker and Rose, 2009) and causing some to rely on pine bark for part of their nutritional needs during the late winter and early spring of 2005 (Nadolny and Rose, 2015). In the last spring, the population did not recover, with numbers dwindling to (probably) below 10/ha in summer. Although the month of lowest numbers was May in the first spring and February in the second spring, there was no hint of even a minor peak of breeding in spring 2005 in our population (not shown in Fig. 1 for the reasons explained in Statistical Analyses in Methods).

The densities we observed (100/ha and 124/ha) are among the highest reported in comparable CMR studies. Schetter et al. (1998), in eastern Oklahoma, recorded peak densities of 90 and 110/ha on 2 grids in year 1 and 55/ha on both grids in year 2; peaks of both years were in August. Wilson et al. (2006), also in eastern Oklahoma, also report highest densities (86/ha) in August, whereas in central Oklahoma peak density (112.5/ha) was achieved in October (Clark et al., 2003). In northern Georgia, highest densities (118/ha and 88/ha) were recorded in May in 2 old fields (Langley and Shure, 1988). In central Florida, peak density of 47/ha was achieved in December, a value that dropped to 10/ha the next month (Stafford and Stout, 1983). Other peak densities were 4.4/ha (Layne, 1974), also in central Florida, and 14/ha across 3 years of study in coastal prairie habitat in Texas (Cameron, 1977). In eastern Kansas, highest densities, reached in

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autumns of 9 years, were about 26–34/ha (Diffendorfer et al., 1995), whereas in a later year the highest density on a control grid was 39.5/ha (Doonan and Slade, 1995); their 2 food-supplemented grids achieved densities of 100–110/ha. In much drier western Kansas, the peak density was 24/ha (Fleharty et al., 1972). In brief, peak density for a region is highly variable, possibly dependent on primary production of the habitat, and is achieved in different seasons, sometimes in summer, more commonly in autumn, but even in winter, as we observed in January 2005. If there is a pattern in these several studies it is that marginal populations, living in more seasonal climates, tend to achieve higher peak densities than the more central populations in Texas and Florida. Furthermore, some studies (e.g., Langley and Shure, 1988) report that severe winter was followed by greatly reduced primary production and the slow recovery of a cotton rat population, further support for the importance of primary production and nutrition.

Tagged cotton rats had a 1:1 sex ratio in our study, but females outnumbered males when we counted the number of tagged animals caught at least once in a month. The most likely explanation for this result is that more females than males were residents and on average females had more captures per individual than males: both were true. In some months, captures of females were much more numerous than males, which is unusual. Male rodents usually have larger home ranges than females and therefore are viewed as being prone to more captures per individual than females. Further, we recorded significantly more transient males than females, an expected result.

Although most studies of cotton rats report sex ratios of unity (e.g., Layne, 1974; Cameron and McClure, 1988; and our study for all tagged animals), Schetter et al. (1998) observed sex ratios of 60–65% males in February and May in both high- and low-density populations in Oklahoma. Goertz (1965), also in Oklahoma, reported male-biased (60%) sex ratios during one May–September period. Joule and Cameron (1980) recorded fluctuating sex ratios, with values sometimes reaching 60% males and at other times 60% females, with no apparent seasonal pattern. During the breeding season, when females (but not males) seek patches of dicots in the Texas coastal prairie (Cameron and Spencer, 2008), even the habitat quality of a grid possibly affects sex ratio. Our population had months and even seasons when females were notably and even significantly more numerous than males; it was as if males had died or emigrated.   For example, in autumn and winter 2003-2004 (Table 2), 95 males and 172 females were recorded, a huge departure from unity. Thus, unlike many species of small mammals, cotton rats seemingly have varying and perhaps fluctuating sex ratios, sometimes within the same population, a pattern awaiting an explanation.

We used a 50-g criterion as the upper limit for juveniles because our earlier necropsy studies had revealed fertile males and pregnant females weighing less than 60 g in populations from southeastern Virginia (Rose and Mitchell, 1990; Bergstrom and Rose, 2004). Our use of a 50-g criterion likely contributed to the low percentage of juveniles (13% for each sex) compared to other studies that used a 60-g criterion, such as Stafford and Stout (1983), who report 28% of males and 40% of females were juveniles in their populations in central Florida. In coastal Texas, Cameron and Kruchek (2005: Fig 4) show juveniles comprising 10–12% of the population in spring and summer but their virtual absence in other seasons. In contrast, Layne (1974), another who used a 50-g criterion, reported 25% juveniles in his population in Florida.

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The faster growth rates in northern populations than in more central ones likely contributes to the generally low proportion of juveniles in marginal populations.

Compared to some other studies, we believe our population had a high proportion of resident cotton rats (Table 2), probably due in part to unsuitable habitat in 3 directions from the grid and a brushy wetland on the fourth. We estimated that proportion by the numbers of resident males and females from each season in Table 2 as a percentage of the row totals. Across the study, about 72 percent of cotton rats were residents, using the criterion of captures in 3 or more months to define a resident. Other investigators have examined transiency patterns; Doonan and Slade (1995) found that 21% of cotton rats were transients on their control grid, and 28% were transients on their food-supplemented grid. Also in eastern Kansas, the percentages of transients ranged from less than 1 to 67 % per month, with the mean being 29 % (Diffendorfer et al., 1995). Among seasons, we observed many fewer transients in winter than in spring or autumn, suggesting that higher proportions of animals were relatively more place-bound in winter.

Cotton rats in southeastern Virginia breed from March through October (Rose and Mitchell, 1990; Bergstrom and Rose, 2004) with occasional extensions by females into November, as happened in 2004, leading to peak density 2 months later. In southeastern Virginia, breeding starts slowly in spring, with the first litters in April and May, but the greatest proportion of breeding females was observed in September and October. Some regional populations have similar patterns. For example, Stafford and Stout (1983) and Layne (1974) found some spring breeding but far greater reproductive activity in autumn in central Florida. In southern Florida, no breeding was detected during the December-May dry season (Smith and Vrieze, 1979). In Oklahoma, Goertz (1965) recorded pregnant females in every month except December and January and a mid-summer lull in breeding. Also in Oklahoma, McMurry et al. (1994) saw high levels (60–100%) of reproduction by females in summer and autumn, with lower levels of breeding in other seasons and none in one spring. In Arkansas, peak breeding from February-July was followed by less reproduction through November (Sealander and Walker, 1955). In eastern Tennessee, winter breeding was rare but breeding peaks were seen in June-July and September-October (Dunaway and Kaye, 1964). In coastal eastern Texas, breeding indices were substantially higher in spring and summer than in the other seasons (Cameron and Kruchek, 2005). The conclusion from reviewing these and other studies of reproduction is that cotton rats have adjusted their breeding seasons to their geographic locations, often starting earlier in the year in the south where a mid-summer lull is common, and with lower levels of breeding in spring by overwintered females than by spring-born females that likely have 1–3 litters in late summer and autumn. Whether our observation, that nearly 100 percent of cotton rats surviving the winter are born in late summer or autumn, is typical of other northern populations remains to be demonstrated.

In theory, high peak densities can be achieved, in part, by lowering the age at first reproduction, a feature observed in some marginal populations. For example, Goertz (1965) found 51 g and 53 g pregnant females in Oklahoma, similar to what has been observed in Virginia (Bergstrom and Rose, 2004; Rose and Mitchell, 1990). Because embryos are not visible until 10 days of pregnancy (Meyer and Meyer, 1944), a 55-g female likely is impregnated when weighing less than 45 g. Future studies may confirm that females from marginal populations begin breeding at lower body masses than those in more central populations.

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Virginia cotton rats are sexually dimorphic, with adult males averaging about 100 g and adult females about 8 g less (Bergstrom and Rose, 2004; Rose and Mitchell, 1990; our study). (Many early studies included the masses of juveniles in the analysis of body mass, thereby greatly lowering mean mass during months of recruitment of young into the population; the more useful comparisons are those that exclude juveniles, whether defined at 50 or 60 g.) In our study, mean seasonal body mass tended to be greatest in spring and lowest in winter; in some seasons the sexes had similar masses (Fig. 2). This pattern is reported for almost all other populations: sexual dimorphism is the rule but in some months the sexes have similar masses. A typical pattern of body mass is seen in coastal Texas (Cameron and Spencer, 1983), with rapid increases in body mass of both sexes in spring, followed by fluctuations in mass, and with mean body mass decreasing in winter.

Several investigators have reported reductions in adult body mass during winter: Chipman in Texas (1966), Goertz (1965) and Schetter et al. (1998) in Oklahoma, Slade et al. (1984) in Kansas, and Dunaway and Kaye (1961, 1964) in Tennessee. In central Florida, adults lose mass starting in October and winter weight loss is as pronounced as in more northerly populations (Layne, 1974). Further, no large adult survived from autumn to spring in Layne's study. Thus, even in central Florida, winter can exact a mass loss and mortality toll. In our population, both sexes nearly held their mean body masses over 3 winters.

The mean lifespans for long-lived males and females in our study are similar to those of previous studies, with several adults living more than 7 months and one female nearly 20 months. Determination of lifespan requires a long trapping history, which is difficult to achieve for a species as vagile as the hispid cotton rat. In his 14-month study in central Florida, Layne (1974) estimated mean residency time for both sexes and all age groups to be 2.9 months. Goertz (1964) reported that half of marked animals disappeared by the second month in Oklahoma and 98% were gone by the 6th month. This is contrasted by 16% of 180 cotton rats surviving for 6 months in Tennessee (Dunaway and Kaye, 1964). Much of gross mortality is attributable to continual movement (leading to emigration out of the study area) rather than to death, but Schnell (1964, 1968) used observational and experimental studies to document losses to a variety of both avian and terrestrial predators as well as natural deaths.

Some investigators (e.g., Goertz, 1965; Layne, 1974) report the loss of large adults as autumn grades into winter, also observed by Odum (1955), who inferred that cotton rat populations may have 2 seasonal cohorts, with few or no spring-born animals surviving the winter and with most long-lived animals being those born in autumn. In our study, no long-lived cotton rat was first caught and tagged from January to July; almost all were tagged between August and November, supporting this conjecture. We believe this pattern supports the argument of spring and fall cohorts in the life cycle of cotton rats. In our population, the fall cohort was long-lived compared to the spring cohort, almost no member of which survived as long as 6 months. Of course, there are exceptions, such as the female in our study that lived through one winter and into the second, and Layne (1974) reporting 2 females tagged in the first month still being alive 14 months later.

In conclusion, our population of *Sigmodon hispidus* in southeastern Virginia was similar in some features to marginal populations in the central states by achieving high annual densities

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in late autumn (rather than in summer) and by having long-lived animals drawn mostly from the autumn cohort, but was different by (nearly) sustaining early winter body mass through the winter, probably due to the moderating effects on winter temperatures of the nearby Chesapeake Bay and Atlantic Ocean. In all, the hispid cotton rat, as a tropical rodent expanding into more temperate locations, is adapting to local conditions by adjusting its peak breeding periods to later in the growing season, perhaps to take advantage of greater plant productivity or nutritional quality of its primarily monocot foods.

LITERATURE CITED

Bergstrom, B. J. and R. K. Rose. 2004. Comparative life histories of Georgia and Virginia cotton rats. Journal of Mammalogy 85:1077-1086.

Cameron, G. N. 1977. Experimental species removal: demographic responses to *Sigmodon hispidus* and *Reithrodontomys fulvescens*. Journal of Mammalogy 58:488-506.

Cameron, G. N. and B. L. Kruchek. 2005. Use of coastal wetlands by hispid cotton rats (*Sigmodon hispidus*). The Southwestern Naturalist 50:397-402.

Cameron, G. N. and P. A. McClure. 1988. Geographic variation in life-history traits of the hispid cotton rat (*Sigmodon hispidus*). Pp. 33-64, *in* Evolution of life histories of mammals. (M. S. Boyce, Ed.). Yale University Press, New Haven, CT. 373 pp.

Cameron, G. N. and S. R. Spencer. 1983. Field growth rates and dynamics of body mass for rodents on the Texas coastal prairie. Journal of Mammalogy 64:656-665.

Cameron, G. N. and S. R. Spencer. 2008. Mechanisms of habitat selection by the hispid cotton rat (*Sigmodon hispidus*). Journal of Mammalogy 89:126-131.

Chipman, R. K. 1966. Cotton rat age classes during a population decline. Journal of Mammalogy 47:138-141.

Clark, J. E., E. C. Hellgren, and E. E. Jorgensen. 2003. Catastrophic decline of a high-density population of hispid cotton rats (*Sigmodon hispidus*) in central Oklahoma. The Southwestern Naturalist 48:467-471.

Diffendorfer, J. E., N. A. Slade, M. S. Gaines, and R. D. Holt. 1995. Population dynamics of small mammals in fragmented and continuous old-field habitat. Pp. 175-199 *In* W. Z. Lidicker (Ed.). Landscape approaches in mammalian ecology and conservation. University of Minnesota Press, Minneapolis.

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Doonan, T. J. and N. A. Slade. 1995. Effects of supplemental food on population dynamics of cotton rats *Sigmodon hispidus.* Ecology 76:814-826.

Dunaway, P. B. and S. V. Kaye. 1961. Cotton rat mortality during severe winter. Journal of Mammalogy 42:265-268.

Dunaway, P. B. and S. V. Kaye. 1964. Weights of cotton rats in relation to season, breeding, and environmental radioactive contamination. American Midland Naturalist 71:141-155.

Fleharty, E. D., J. R. Choate, and M. A. Mares. 1972. Fluctuations in population density of the hispid cotton rat: factors influencing a "crash." Bulletin of the Southern California Academy of Science 71:132-138.

Goertz, J. W. 1964. The influence of habitat quality upon density of cotton rat populations. Ecological Monographs 34:359-381.

Goertz, J. W. 1965. Sex, age and weight variation in cotton rats. Journal of Mammalogy 46:471-477.

Green, H. A. and R. K. Rose. 2009. Growth and survival in a northern population of hispid cotton rats. Journal of Mammalogy 90:851-858.

Hines, J.E. 1996. JOLLY software to compute estimates of survival and capture probability models. United States Geological Survey–Patuxent Wildlife Research Center. http://www.mbr-pwrc.usgs.gov/software/specrich.html. Accessed December 2006.

Joule, J. and G. N. Cameron. 1980. Demographic studies of sympatric *Sigmodon hispidus* and *Reithrodontomys fulvescens*. American Midland Naturalist 103:47-58.

Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs 36:239-273.

Langley, A. K., Jr. and D. J. Shure. 1988. The impact of climatic extremes on cotton rat (*Sigmodon hispidus*) populations. American Midland Naturalist 120:136-143.

Layne, J. N. 1974. Ecology of small mammals in a flatwoods habitat in north-central Florida, with emphasis on the cotton rat (*Sigmodon hispidus*). American Museum Novitates 2544:1-48.

McMurry, S. T., R. L. Lochmiller, J. F. Boggs, D. M. Leslie, Jr., and D. M. Engle. 1994. Demographic profiles of populations of cotton rats in a continuum of habitat types. Journal of Mammalogy 75:50-59.

Meyer, B. J. and R. K. Meyer. 1944. Growth and reproduction of the cotton rat, *Sigmodon hispidus hispidus*, under laboratory conditions. Journal of Mammalogy 25:107-129.

Nadolny, R. M. and R. K. Rose. 2015. Girdling by the hispid cotton rat as a significant source of mortality in a loblolly pine (*Pinus taeda*) successional forest. American Midland Naturalist 174:74-86.

Odum, E. P. 1955. An eleven year history of a *Sigmodon* population. Journal of Mammalogy 36:368-378.

Pagels, J. F. and N. D. Moncrief. 2015. Virginia's land mammals: past and present, with some thoughts about their possible future. Virginia Journal of Science 66:171-222.

Patton, C. P. 1941. The eastern cotton rat in Virginia. Journal of Mammalogy 22:91.

Rose, R. K. 1994. Instructions for building 2 live traps for small mammals. Virginia Journal of Science 45:151-157.

Rose, R. K. and M. H. Mitchell. 1990. Reproduction in the hispid cotton rat *Sigmodon hispidus* Say and Ord (Rodentia: Muridae) in southeastern Virginia. Brimleyana 16:43-59.

Sauer, J. R. 1985. Mortality associated with severe weather in a northern population of cotton rats. American Midland Naturalist 113:188-189.

Schetter, T. A., R. L. Lochmiller, D. M. Leslie, Jr., D. M. Engle, and M. E. Payton. 1998. Examination of the nitrogen limitation hypothesis in non-cyclic populations of cotton rats (*Sigmodon hispidus*). Journal of Animal Ecology 67:705-721.

Schnell, J. H. 1964. A mink exterminates an insular cotton rat population. Journal of Mammalogy 45:305-306.

Schnell, J. H. 1968. The limiting effects of natural predation on experimental cotton rat populations. Journal of Wildlife Management 32:698-711.

Sealander, J. A. and B. Q. Walker. 1955. A study of the cotton rat in northwestern Arkansas. Proceedings of the Arkansas Academy of Science 8:153-162.

Sikes, R.S. and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663-688.

Slade, N. A., J. R. Sauer, and G. E. Glass. 1984. Seasonal variation in field-determined growth rates of the hispid cotton rat (*Sigmodon hispidus*). Journal of Mammalogy 65:263-270.

Smith, A. T. and J. M. Vrieze. 1979. Population structure of Everglades rodents: responses to a patchy environment. Journal of Mammalogy 60:778-794.

SPSS, Inc. 2003. SPSS base 12.0 for Windows user's guide. SPSS, Inc. Chicago, Illinois.

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Stafford, S. R. and I. J. Stout. 1983. Dispersal of the cotton rat, *Sigmodon hispidus*. Journal of Mammalogy 64:210-217.

Stickel, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. Journal of Mammalogy 35:1-15.

Walker, L. A. and R. K. Rose. 2009. Seasonal variation in the diet of a marginal population of the hispid cotton rat, *Sigmodon hispidus*. Virginia Journal of Science 60:3-11.

Wilson, J. A., R. L. Lochmiller, and D. M. Janz. 2006. Population dynamics of cotton rats (*Sigmodon hispidus*) inhabiting abandoned petroleum landfarms in Oklahoma, USA. Ecotoxicology 15:19-30.

TABLE 1. Total numbers of small mammals caught in live traps from December 2002 through February 2005 in Chesapeake, southeastern Virginia. Each number is the sum of the different tagged animals caught each month and the number in parenthesis includes recaptures within a month. Sex could not be determined for the shrews and a few immature rodents.

Species	Males	Females	Unknown	Total
Sigmodon hispidus	538 (694)	652 (874)	0	1190 (1568)
Microtus pennsylvanicus	141 (181)	124 (153)	1	266 (335)
Reithrodontomys humulis	96 (104)	90 (115)	0	186 (219)
Mus musculus	43 (44)	19 (19)	1	63 (64)
Oryzomys palustris	20 (25)	14 (14)	1	35 (40)
Cryptotis parva	—	—	11	11 (11)
Blarina sp.	—	—	6	6 (6)
Microtus pinetorum	1 (2)	3 (3)	0	4 (5)
Total	839 (1050)	902(1178)	20	1761 (2248)

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TABLE 2. Numbers of male and female *Sigmodon hispidus* that were transients, visitors, and residents as recorded in different seasons in Chesapeake, southeastern Virginia. Transients were observed in only one month, visitors in 2 consecutive months, and residents for at least 3 months on the grid. We estimated the percentage of residents in each season by dividing the numbers of residents from each season by the row totals; more than half of tagged cotton rats were residents in every season.

| Season	Transients		Visitors		Residents		% Residents
	Males	Females	Males	Females	Males	Females	
Winter 2002-2003	19	26	13	10	50	44	58
Spring 2003	9	9	5	4	47	45	77
Summer 2003	12	7	5	0	34	35	74
Autumn 2003	16	14	15	12	68	102	75
Winter 2003-2004	10	10	8	9	27	70	72
Spring 2004	20	3	3	1	18	34	66
Summer 2004	16	6	0	14	25	34	62
Autumn 2004	14	9	18	11	77	90	76
Winter 2004-2005	13	6	8	14	82	89	81
Total/Mean	129	90	75	75	428	543	72
Grand total	219		150		971		

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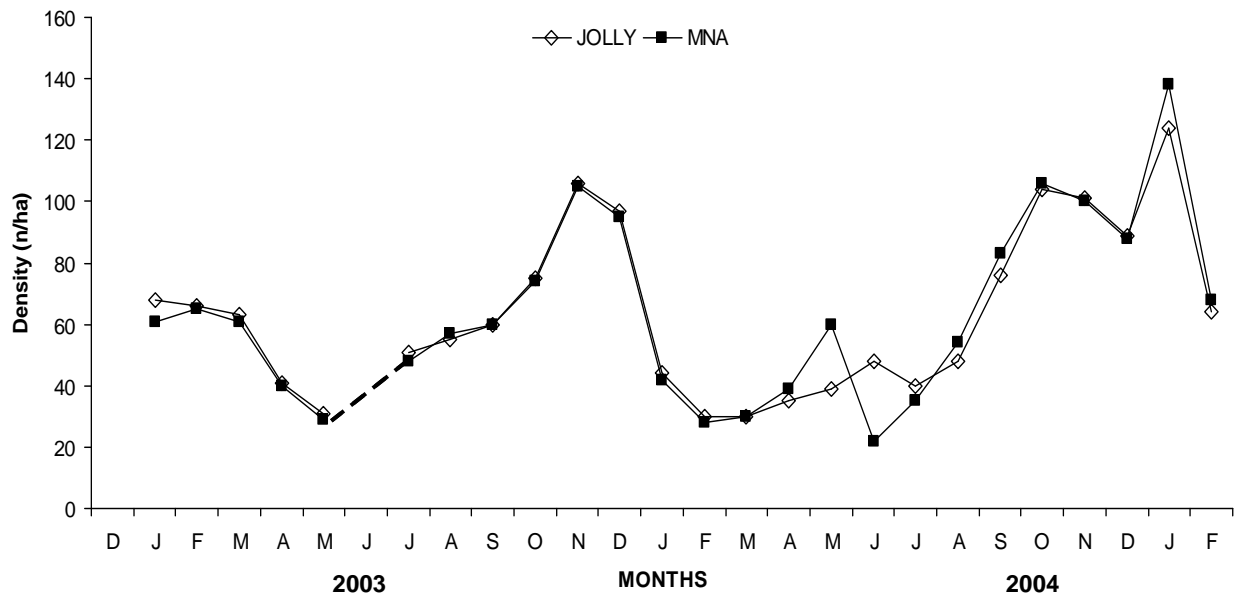
FIGURE 1. Monthly estimates of population density of *Sigmodon hispidus* from December 2002 to February 2005 in Chesapeake, southeastern Virginia. Density (*n*/ha) was determined by the software package JOLLY and by minimum number alive (MNA) methods. Dashed lines represent the gap in data collection for June 2003. Increases in density were observed in both autumns and slightly in the spring of 2004.
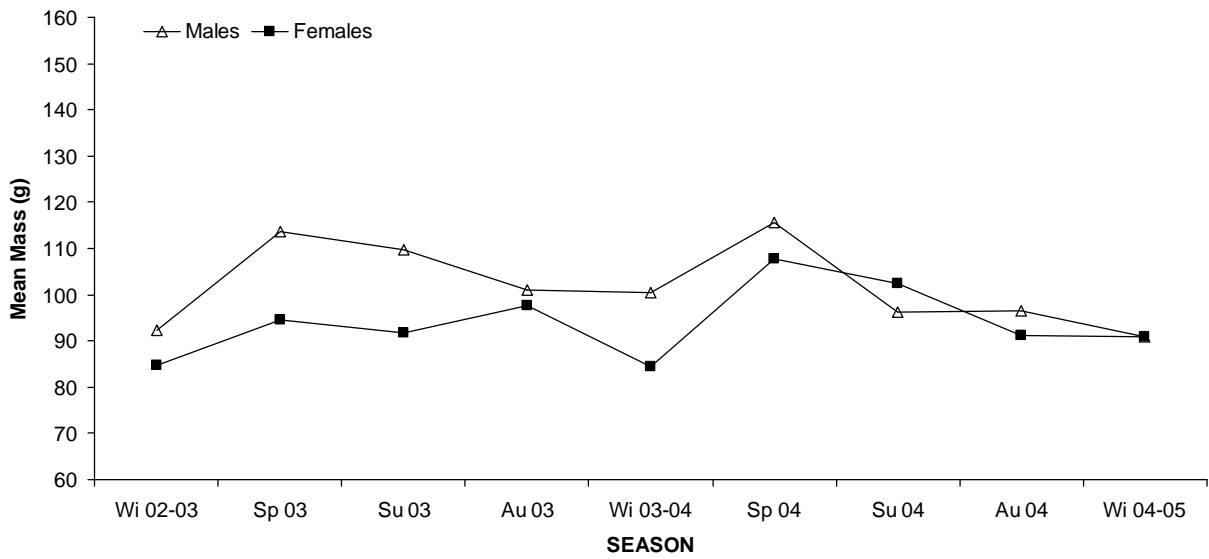
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FIGURE 2. Mean masses (g) for sub-adult and adult male and female *Sigmodon hispidus* in the 4 seasons in Chesapeake, southeastern Virginia. Large increases in mean mass for both sexes were observed from winter into spring, followed by a decline in mean mass later. Pregnant females were excluded from analysis.

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